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Dietary niche overlap and prey consumption for the Steller sea lion (*Eumetopias jubatus*) and California sea lion (*Zalophus californianus*) in northwest Washington during 2010–2013

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Abstract—The diets of Steller (*Eumetopias jubatus*) and California (*Zalophus californianus*) sea lions in northwest Washington are poorly documented. We hypothesized that these species exploit the same prey in Washington because they are both generalist predators that utilize the same haul-out sites and are similar in behavior and body size. We analyzed 776 samples of scat from Steller sea lions and 263 samples of scat from California sea lions collected throughout each year during 2010–2013. The aim of this analysis was to characterize seasonal and annual diets, estimate biomass of prey consumed, and evaluate dietary niche overlap. Steller and California sea lions ate diverse diets that varied seasonally and annually. Primary prey groups for both sea lion species were Clupeidae, Salmonidae, Sebastidae, Rajidae, Pleuronectiformes, Squalidae, and Merlucciidae. We estimated that Steller sea lions ate 11,327 metric tons (t) (standard deviation [SD] 1600) and that California sea lions ate 9063 t (SD 4098) of prey per year during our study. We found significant dietary niche overlap between California and Steller sea lions that feed in northwest Washington.

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The diets of California (*Zalophus californianus*) and Steller (*Eumetopias jubatus*) sea lions have been studied in much of the California Current Ecosystem, yet notable knowledge gaps exist. Diets of populations of California sea lions have been studied at the Channel Islands (Antonelis et al., 1984; Lowry et al., 1991; Lowry and Carretta, 1999; Orr et al., 2011), the Farallon Islands (Bailey and Ainley, 1981), and Monterey Bay (Weise and Harvey, 2008) in California. However, California sea lions, predominately males (Gearin et al., 2017), are distributed north of California as far as Alaska (Maniscalco et al., 2004). Diets of California sea lions north of California are poorly documented with only 2 peer-reviewed published studies (Everitt et al., 1981; Roffe and Mate, 1984) and 3 reports (Reimer and Brown[1]; Scordino[2]; Trites and Rosen[3]). Likewise, the diet of Steller sea lions has been studied in Oregon and Northern California (Riemer et al., 2011), but in Washington it has been reported only in gray literature (Scordino[2]; Wiles, 2015).

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[1] Riemer, S. D., and R. F. Brown. 1997. Prey of pinnipeds at selected sites in Oregon identified by scat (fecal) analysis, 1983–1996. Oregon Dep. Fish Wildl., Tech. Rep. 97-6-02, 34 p. [Available from Oregon Dep. Fish Wildl. Mar. Reg., 4034 Fairview Industrial Dr. SE, Salem, OR 97302.]

[2] Scordino, J. 2010. West Coast pinniped program investigations on California sea lion and Pacific harbor seal impacts on salmonids and other fishery resources, 97 p. Pac. States Mar. Fish. Comm., Portland, OR. [Available from website.]

[3] Trites, A. W., and D. A. S. Rosen (eds.). 2019. Synthesis of scientific knowledge and uncertainty about population dynamics and diet preferences of harbour seals, Steller sea lions and California sea lions, and their impacts on salmon in the Salish Sea. Technical workshop proceedings, May 29–30, 2019, 67 p. Mar. Mamm. Res. Unit, Univ. B. C., Vancouver, Canada. [Available from website.]

Better knowledge of the spatial and temporal variability of the diets of California and Steller sea lions is needed.

It is likely that California and Steller sea lions utilize the same marine environment for hunting prey because the sympatric species use the same haul-out sites (Mate, 1975) and because adult male California sea lions are similar in size to adult female Steller sea lions and, therefore, have similar physiological limits to dive performance (Weise et al., 2010). It is noteworthy that, although the abundance of the eastern distinct population segment of Steller sea lions increased at an annual rate of 4.25% for pups and of 3.22% for age-1+ sea lions from 1987 to 2017 (Muto et al., 2020), the growth rate of the population was not uniform across its range. The range of the Steller sea lion has contracted northward since the early 20th century with rookeries abandoned in Southern California and abundance at rookeries in central California declining significantly (Pitcher et al., 2007; NMFS, 2013). One hypothesis is that niche competition with California sea lions, which were increasing in abundance (Laake et al., 2018), caused the range contraction (Mate, 1975; NMFS, 2013). Understanding to what degree the dietary niches of California and Steller sea lions overlap will improve our understanding of the ecology of the 2 species and the potential for competition between them.

In this study, we had 3 objectives to advance our knowledge of the diets of California and Steller sea lions in northwest Washington. First, we characterized the diets of both species, including documenting prey diversity and seasonal and annual variability in diet. Second, we performed calculations to estimate the biomass (in metric tons) of fish and invertebrates consumed per year and season by California and Steller sea lions. Last, we used our diet data to evaluate the hypothesis that these sympatric sea lion species have significant dietary niche overlap.

Materials and methods

Study area

Study activities were conducted in northwest Washington (Fig. 1), which is the northernmost extent of the California Current. Relative to other portions of the northern California Current, the waters of northwest Washington have elevated productivity and enhanced biomass of high trophic levels due to geomorphic features and the confluence of the California Current and the Strait of Juan de Fuca (McFarlane et al., 1997; Marchetti et al., 2004; MacFadyen et al., 2008). Year-round sea lion haul-out sites in the study area include the Tatoosh Island Complex (haul-out sites: Tatoosh Island East, Tatoosh Island Cut, and Duncan Rock), Bodelteh Island Complex (haul-out sites: East Bodelteh Island, West Bodelteh Island, Umatilla Reef, and Guano Rock), Carroll Island, and Sea Lion Rock (Fig. 1). At Carroll Island and Sea Lion Rock, 10–20 Steller sea lion pups were born each year during the study period of 2010–2013; both sites now meet the definition of a rookery (Pitcher et al., 2007) with greater than 50 newborn pups counted annually at Carroll Island since 2015 and Sea Lion Rock since 2019 (senior author, unpubl. data). We also surveyed Waadah Island, which is a seasonal haul-out site primarily utilized in the spring.

Field methods

Haul-out counts Vessel-based surveys were conducted by circling haul-out sites and counting sea lions with 7×50 or 8×40 binoculars. When possible, we conducted land-based surveys of East Bodelteh Island. Sea lions at haul-out sites were counted in sections because of the size of the sites and to minimize disturbance by only circling each site once. For each section, we counted the total number of Steller and California sea lions present, and then we recounted the section for 4 demographic groups of Steller sea lions: pups, juveniles, adult females, and adult males. Pups were identified by their darker brown color, chubbier features, and smaller size and were counted from birth (May–July) through 11 months of age (May) (Pitcher et al., 2001). Juveniles were identified as individuals older and larger than pups that had not developed the secondary sexual characteristics of adult males or the size of adult females and were assumed to be between 1 and roughly 5 years of age. Adult females were identified by size, shape, and presence of a pup or dependent juvenile and by having longer whiskers than juveniles (King et al., 2007; Stricker et al., 2015). Adult males were identified by their overall larger size, coarse fur on chest and neck, and large head and foreflippers.

We used the known age of branded individuals (see Wright et al., 2017) to calibrate our methods for classifying demographic groups. No demographic count was assigned if the sea lions entered the water or were arranged too close together to evaluate body shape. We assumed all California sea lions were adult males even though we did observe at least one female identified by the presence of a newborn pup and many juveniles including one that was identified as a 1 year old from San Miguel Island, California, on the basis of its brand number (see DeLong et al., 2017).

We used the demographic counts to calculate the proportion of age-1+ Steller sea lions observed that were adult male, adult female, and juvenile; pups and sea lions not classified to a demographic group were excluded from this calculation. Olesiuk[4] found no significant difference in the proportion of time that age-1+ sea lions spent hauled out by sex or age, indicating that our demographic counts of age-1+ sea lions that were hauled out are representative of the whole population that utilized haul-out sites in northwest Washington during surveys.

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[4] Olesiuk, P. F. 2018. Recent trends in abundance of Steller sea lions (*Eumetopias jubatus*) in British Columbia. Can. Sci. Advis. Secr. Res. Doc. 2018/006, 67 p. [Available from website.]

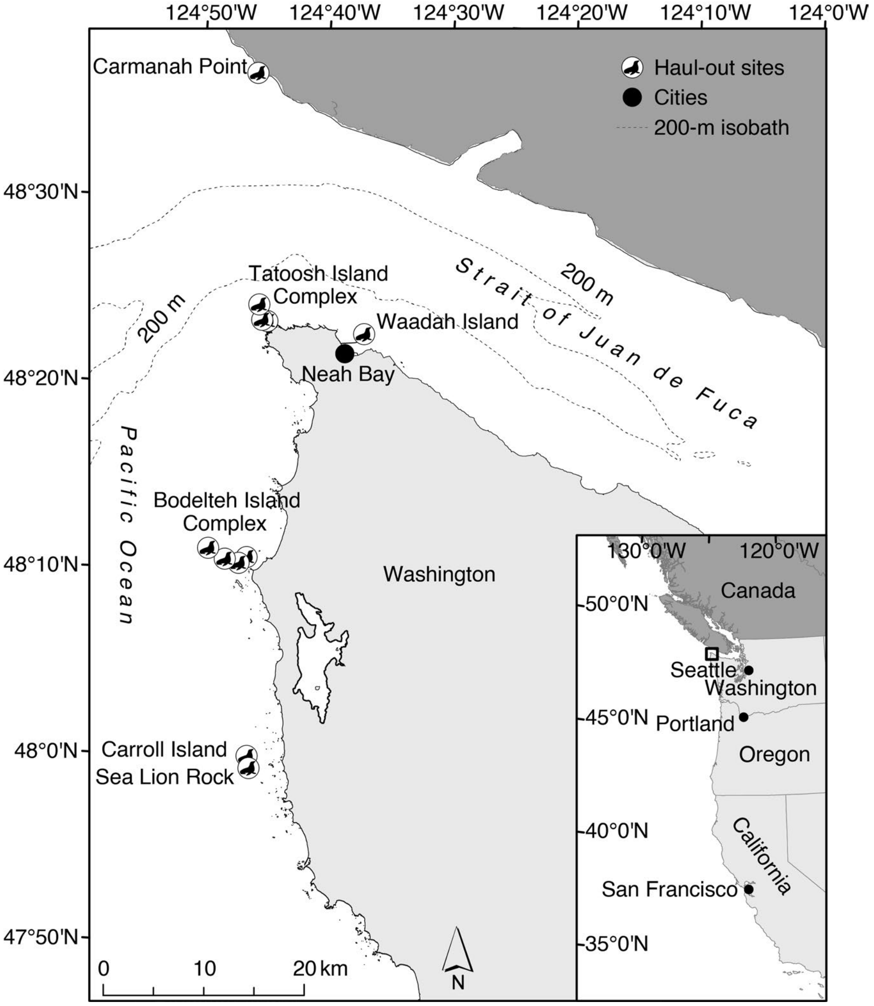

Figure 1

Map of study area of northwest Washington marking haul-out sites of Steller sea lions (*Eumetopias jubatus*) and California sea lions (*Zalophus californianus*) where counts of sea lions and scat collections occurred from 2010 through 2013. The dotted line indicates the 200-m isobath.

Counts of the age-1+ population were included in this analysis only if sea lions at all the haul-out sites in the survey area were counted and, for Steller sea lions, only if a full demographic count was conducted. The exception was that if we had a land-based count for East Bodelteh Island within 10 d of a survey that included all haul-out sites, we used the land-based count for East Bodelteh Island rather than the boat-based count for that day. The counts are minimum estimates of sea lions present because an unknown proportion of the sea lions that were hauled out were not visible during the surveys and, therefore, were not counted (Westlake et al., 1997). We used average counts, rather than maximums, because both species of sea lions are known to change their distribution in response to prey and other factors (Sigler et al., 2009; Womble et al., 2009; Olesiuk[4]; Brown et al., 2020).

Scat collection We collected scat from the Tatoosh Island Complex, Bodelteh Islands Complex, Carroll Island, and Sea Lion Rock (Fig. 1). Locations of scat collections differed by season and were influenced by sea conditions, safety of transferring staff onto the haul-out site, and haul-out utilization by sea lions. Samples of scat of California sea lions were primarily collected at East Bodelteh Island, where large aggregations of California sea lions occur in the spring, early summer, and fall. A central assumption to our sampling method was that scat collected from any haul-out site in northwest Washington was representative of scat of Steller and California sea lions at all haul-out sites in northwest Washington.

Scat samples were collected following procedures described by Lance et al.[5] We were careful to ensure that we collected each scat in its entirety, we avoided collecting scat where multiple scats were likely to be mixed together, and we targeted fresh scat (Akmajian et al., 2017) to minimize potential biases (Staniland, 2002; Bowen and Iverson, 2013). Our goal was to collect 30 scats of Steller sea lions per month and 50 scats of California sea lions per season from August 2010 through February 2013. We defined seasons as follows: December–February as winter, March–May as spring, June–August as summer, and September–November as fall. We targeted haul-out sites, or sections of these locations, where greater than 95% of the sea lions counted at the site were of the species targeted for scat collections. Scats of California sea lions were collected only during the spring, summer, and fall; the difficulty of landing on East Bodelteh Island in winter meant no samples could be collected from the few California sea lions that remained at the site.

Sample processing and prey identification

Scat samples were washed in a residential-style washing machine or through nested sieves by using published procedures (Lance et al.[5]; Orr et al., 2003). Prey hard parts collected from the scat were dried and stored in glass vials. All identifiable hard parts (e.g., bones, otoliths, cartilaginous parts, lenses, teeth, and cephalopod beaks) recovered from scat were examined by using a dissecting microscope and identified to the lowest possible taxon to reduce identification biases (Browne et al., 2002). Prey remains were identified by S. Riemer (of the Oregon Department of Fish and Wildlife, Marine Mammal Program), who used a reference collection of fish and cephalopods from the northeastern Pacific Ocean and coastal estuaries (see Riemer et al., 2011).

Diet analysis

Diet reconstruction We used split-sample frequency of occurrence (SSFO) to reconstruct diets of sea lions because the method produces results that are very similar to volumetric estimates of the composition of prey species in the diets of predators (Olesiuk et al., 1990) because SSFO can be easily incorporated into ecological indices (Krebs, 1999) and because it requires only data on presence and absence of prey (Laake et al., 2002; Tollit et al., 2007). The SSFO approach assumes recovery of remains from all prey consumed and consumption of all prey at an equal volume (Olesiuk et al., 1990). Split-sample frequency of occurrence was calculated by using the following formula:

$$SSFO_{\mathrm{i}} = \frac{\sum_{\mathrm{k=1}}^{\mathrm{i}} \left(O_{\mathrm{ik}} / O_{\mathrm{k}} \right)}{s} \times 100, \qquad (1)$$

where $SSFO_{\mathrm{i}}$ = SSFO of taxon i;

O_{ik} = the absence (0) or presence (1) of taxon i in fecal sample k;
O_{k} = the total number of all taxa present in fecal sample k; and
s = the total number of fecal samples that contained identifiable prey.

We present values of frequency of occurrence (FO) in Supplementary Table 1 to allow comparison to past studies. The following formula was used to calculate FO:

$$FO_{\mathrm{i}} = \frac{\sum_{\mathrm{k=1}}^{\mathrm{s}} O_{\mathrm{ik}}}{s} \times 100, \qquad (2)$$

where FO_{i} = the FO of taxon i.

We used 2 definitions of prey taxon. For reporting what prey sea lions ate, prey taxon was defined as the lowest taxon to which a prey item was identified. For calculating ecological indices of diet diversity and dietary niche overlap, we defined prey taxa by prey family, with the exception of flatfish, which were defined by order, and cephalopod and amphibian remains, which were defined by class, because these groups could not be accurately identified to the family level (Sinclair and Zeppelin, 2002). We considered taxa that had an SSFO of 5% or greater to be common prey.

Prey diversity and overlap indices We characterized prey diversity for the 2 sea lion species by using 2 indices: Levin's niche breadth and the Shannon–Wiener diversity index. Levin's niche breadth is sensitive to changes in abundant species, and the Shannon–Wiener index is sensitive to changes in rare species (Krebs, 1999). We used this formula to obtain Levin's niche breadth values (D): $\frac{1}{D}$, where D is $\sum_{\mathrm{i}} p_{\mathrm{i}}^2$ and p_{i} is the SSFO of taxon i. We used this formula to obtain the Shannon–Wiener diversity index values (H):

$$H = -\sum_{\mathrm{i}} (p_{\mathrm{i}} \times \ln(p_{\mathrm{i}})). \qquad (3)$$

We used the Morisita–Horn index (Horn, 1966; Krebs, 1999) to compare dietary niche overlap of Steller and California sea lions because it is reported to have the least bias among indices in comparison of diets when prey proportions (like SSFO) are used (Smith and Zaret, 1982). Morisita–Horn index values (MH) were obtained by using the following formula:

$$MH = \frac{2\sum p_{\mathrm{ij}} p_{\mathrm{ik}}}{\sum p_{\mathrm{ij}}^2 + \sum p_{\mathrm{ik}}^2}, \qquad (4)$$

where p_{ij} = the SSFO of prey taxon i for population j; and
p_{ik} = the SSFO of prey taxon i for population k.

Dietary niche overlap varies along a scale from 0 to 1, with 1 indicating a complete overlap and 0 indicating no overlap. We considered a value of 0.65 or greater to indicate

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[5] Lance, M. M., A. J. Orr, S. D. Riemer, M. J. Weise, and J. L. Laake. 2001. Pinniped food habits and prey identification techniques protocol. Alaska Fish. Sci. Cent., AFSC Process. Rep. 2001-04, 29 p. [Available from website.]

significant niche overlap (see Aurioles-Gamboa and Camacho-Ríos, 2007; Orr et al., 2011).

To accompany the prey diversity and niche overlap indices, we obtained corresponding 95% nonparametric bias-corrected and accelerated bootstrap confidence intervals using 5000 bootstrap samples. The bias-corrected and accelerated bootstrap confidence interval takes into account potential bias and skewness in a bootstrap sampling distribution (DiCiccio and Efron, 1996). The package boot (vers. 1.3-20; Davison and Hinkley, 1997; Canty and Ripley, 2017) was used in statistical software R (vers. 3.6.2; R Core Team, 2019) to calculate each bootstrap sample, bootstrap sampling distribution, and bootstrap confidence interval. Each bootstrap sample was taken with replacement within a given sampling strata.

Prey consumption model

We developed models to estimate average seasonal and annual prey consumption for Steller and California sea lions by using published data sources and data collected during this study for sea lions in northwest Washington for the period from 2010 through 2013.

Simply stated, the model multiplies an estimate of prey consumed per individual per day by the total number of sea lions present in the study area and extrapolates out, by using the number of days in the season, to estimate total prey consumed each season (see Equation 5). We estimated consumption for spring (March–May), summer (June–August), fall (September–November), and winter (December–February) for both California and Steller sea lions. Added together, the seasonal estimates provide a yearly estimate of total consumption for each sea lion species.

To determine annual prey consumption by California and Steller sea lions in northwest Washington during 2010–2013, we used the following equation:

$$\sum_x \sum_y \sum_z (w_{y,z} \times c_{y,z} \times d_x \times n_{x,y} \times p_{x,y,z} \times f_{x,y}) / 1000, \qquad (5)$$

where x = season;
y = the species of sea lion (California or Steller sea lion);
z = the demographic group (adult male, adult female, juvenile male, and juvenile female for Steller sea lions and adult males for California sea lions);
$w_{y,z}$ = the estimated average body weight in kilograms of sea lions of species y and demographic group z.
$c_{y,z}$ = a conditional parameter for the percentage of body weight that the average sea lion of species y and demographic group z eats per day.
d_x = the number of days in season x;
$n_{x,y}$ = the average count of age-1+ sea lions hauled out in the survey area during season x for species y;
$p_{x,y,z}$ = the proportion of sea lions counted in season x, of species y and demographic group z.; and
$f_{x,y}$ = the correction factor for converting the haul-out count to the total abundance of sea lions in the environment of northwest Washington during season x for species y.

California sea lion average body weight was informed by the average body weight of male California sea lions captured at Astoria, Oregon (Wright et al., 2010), and Ballard, Washington (Gearin et al., 2017). The $w_{y,z}$ for Steller sea lions was informed by published body weight estimates for demographic group z (Winship et al., 2001).

The conditional parameter $c_{y,z}$ was informed by published bioenergetics modeling estimates of Winship et al. (2006) for male California sea lions and by demographic group z for Steller sea lions. The bioenergetics models of Winship et al. (2006), the methods of which are described in greater detail in Winship et al. (2002), incorporate energetic costs for lactation and gestation.

The average count of age-1+ sea lions was informed by our surveys as previously described.

We assumed that California sea lions composed a single male demographic group. The $p_{x,y,z}$ for adult female and adult male Steller sea lions were informed directly by the haul-out demographic counts. We were unable to differentiate juvenile Steller sea lions by sex during counts and had to calculate the expected proportion of juveniles that were male or female on the basis of sex-based survival estimates through age 5 for Steller sea lions branded in Northern California and southern Oregon (Wright et al., 2017), assuming an equal sex ratio at birth.

We used a correction factor developed by Lowry and Forney (2005) for counts of California sea lions from aerial surveys at haul-out sites in Northern California. For Steller sea lions, we used the reciprocal of the proportion of age-1+ sea lions hauled out in southern British Columbia (Olesiuk[4]). Olesiuk[4] reported that 36% (coefficient of variation [CV]=2.1%) of age-1+ sea lions were hauled out in winter during the time frame of 1000–1800, when our surveys were typically conducted, and they reported that 67.4% (CV=5.6%) of age-1+ sea lions were hauled out in summer. We applied the winter correction factor for Steller sea lions to the spring and fall because Olesiuk[4] found no significant difference in the proportion of time that satellite-tagged sea lions hauled out in the spring and winter and because Whitlock et al. (2020) found much lower haul-out attendance in the spring than in the summer. The correction factors calculated from data presented by Olesiuk[4] fall within the range and seasonality of the proportion of sea lions observed hauled out by Whitlock et al. (2020). No correction factors were applied for sea lions missed by vessel- or land-based surveys that would have been visible and counted during aerial surveys (Westlake et al., 1997) because no correction values were available in the literature. Likewise, no correction factors were applied to estimate the number of sea lions that were using haul-out sites off southern Vancouver Island, British Columbia, and that would forage in the same marine area as the sea lions that were using haul-out sites in northwest Washington.

We divided our total consumption estimate by 1000 to convert our estimate from kilograms to metric tons.

Table 1

Summary of the sampling of scat of Steller sea lions (*Eumetopias jubatus*) and California sea lions (*Zalophus californianus*) conducted from 2010 through 2013 in northwest Washington, by year, season, and month.

		No. of samples												
		Spring			Summer			Fall			Winter			
Species	Year	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Total
Steller sea lion	2010	0	0	0	0	0	32	3	0	27	0	0	0	62
	2011	48	18	24	35	36	42	4	31	36	0	38	0	312
	2012	38	35	34	28	36	38	35	22	38	8	0	39	351
	2013	0	0	0	0	0	0	0	0	0	0	34	17	51
California sea lion	2010	0	0	0	0	0	0	42	0	0	0	0	0	42
	2011	0	0	47	2	0	0	0	0	51	0	0	0	100
	2012	0	0	0	48	0	0	51	22	0	0	0	0	121

Monte Carlo simulations were used to incorporate uncertainty in estimating prey consumption by California and Steller sea lions. In each run of the model, parameter values were randomly selected from the parameter sampling distributions listed in Supplementary Table 2 for California sea lions and in Supplementary Table 3 for Steller sea lions. The simulation was run in R 10,000 times to estimate the mean and standard deviation (SD) of the total mass of prey consumed by California and Steller sea lions. We developed and used R code for estimating prey consumption by sea lions (the code is available from website).

We multiplied our seasonal prey consumption estimates by the SSFO of each prey taxon to estimate the average metric tons eaten by sea lions in each season. Because we had no winter diet data for California sea lions, we used the pooled SSFO from all scat collections to estimate the amount eaten in winter. Seasonal estimates were added together to obtain annual consumption of each prey type by each sea lion species.

Results

During the study, 776 scat samples from Steller sea lions and 263 scat samples from California sea lions were collected (Table 1). Collections of scat of Steller sea lions were conducted primarily at the Tatoosh Complex in winter, Sea Lion Rock in summer, and a mix of all sites in spring and fall (Suppl. Table 4). The majority of scats from California sea lions were collected at East Bodelteh Island, with 2 collections totaling 13 samples taken at Carroll Island. All raw count data from haul-out surveys and results from scat analysis are publicly available (Scordino et al.[6]).

Counts of sea lions

Counts indicate very different patterns in utilization of haul-out sites by California and Steller sea lions in northwest Washington (Fig. 2). Steller sea lions were present throughout the year with slightly greater counts in fall and slightly lower counts in winter. The greatest counts of California sea lions were recorded in fall. The proportion of the population of Steller sea lions composed of adult males, adult females, juveniles, and pups was variable by month, with adult females and juveniles accounting for the majority of counts (Fig. 3). The exception was during summer when males composed a percentage of the hauled-out population similar to that for adult females. For individual haul-out sites within the study area, counts reveal variable patterns in utilization by sea lion species (Suppl. Figs. 1–7) and by demographic group of Steller sea lions (Suppl. Figs. 8–14).

Diet of Steller sea lions

The primary prey groups (those with SSFO >5%) for all scat samples from Steller sea lions were Clupeidae (22.7%), Sebastidae (14.0%), Rajidae (13.1%), Salmonidae (11.7%), Pleuronectiformes (9.7%), Squalidae (8.3%), and Merlucciidae (5.6%) (Table 2).

For Steller sea lions, diet varied between seasons both in the SSFO of common prey species and diet diversity indices. Diet diversity was similar in spring and fall and in summer and winter, with the greatest diversity occurring in spring and fall for all measures (Table 3). The Levin's niche breadth values are likely driven by the fact that the 3 most common prey families in the spring and fall made up 47.5% and 47.1% of the Steller sea lion diet, respectively; whereas, the 3 most common prey families in the summer and winter made up 62.6% and 61.4% of the diet, respectively (Table 2). Pacific hake (*Merluccius productus*) were common in the summer (10.8%) and fall (8.5%) but rarely consumed in the

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[6] Scordino, J., A. Akmajian, and S. Riemer. 2021. Steller and California sea lion count and diet data in northwest Washington, 2010–2013. Mendeley Data, V1. [Available from website.]

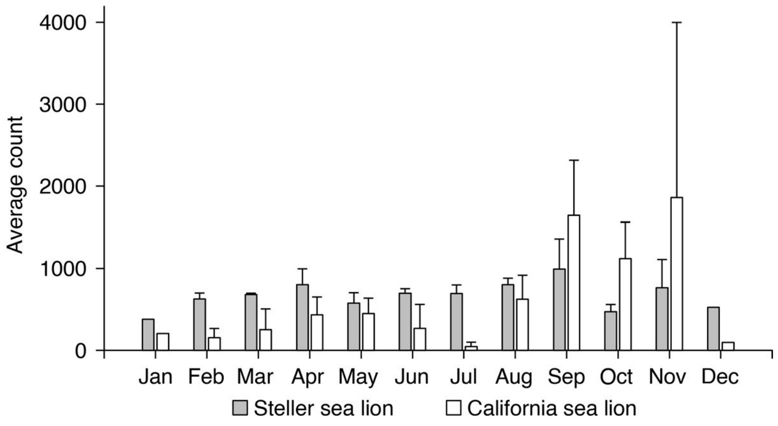

Figure 2

Average monthly counts of age-1+ Steller sea lions (*Eumetopias jubatus*) and California sea lions (*Zalophus californianus*) in northwest Washington during vessel- and land-based surveys conducted from 2010 through 2013. Error bars indicate standard deviations.

winter (0.3%) and spring (0.9%). Conversely, consumption of Gadidae was low in the summer (1.7%) and fall (3.6%) but common in the winter (5.7%) and spring (9.0%). Pleuronectiformes were common in all seasons (>5%) except winter. Clupeidae was the most common prey family in the diet of Steller sea lions in summer with an SSFO of 36.7% but accounted for only 13.8% of the diet in spring, likely driven by the presence of Pacific sardine (*Sardinops sagax*), which had an SSFO of 18.5% in summer but was rarely consumed in other seasons.

Annual comparisons of diet included only data from 2011 and 2012 because samples were collected in all seasons (Table 1). Diet diversity was greater in 2012 than in 2011 for both measures (Table 3). Consumption of common prey species also varied between years. The SSFO of Clupeidae declined from 27.9% in 2011 to 20.1% in 2012, likely due to a large reduction in the consumption of Pacific sardine. From 2011 to 2012, the consumption of northern anchovy (*Engraulis mordax*) and Pacific hake also declined. In 2012, Steller sea lions had higher consumption of common prey taxa, including Pleuronectiformes, Salmonidae, and Pacific spiny dogfish (*Squalus suckleyi*), and increases in consumption of a number of less common prey taxa, in comparison to levels in 2011 (Suppl. Table 5).

Diet of California sea lions

The primary prey families (>5% SSFO) for all scat samples from California sea lions were Clupeidae (38.2%),

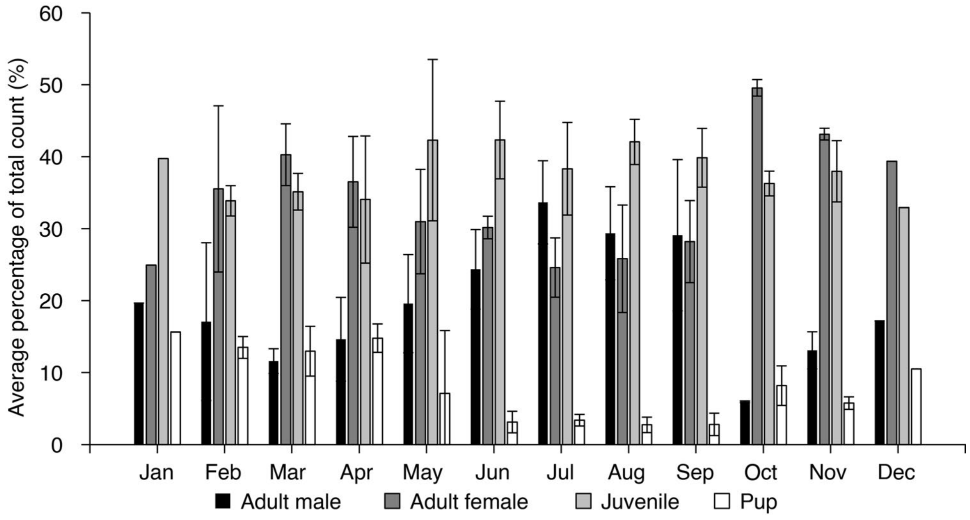

Figure 3

Average monthly percentage of counts of Steller sea lions (*Eumetopias jubatus*) at haul-out sites during 2010–2013 in northwest Washington for 4 demographic groups. The demographic groups used in counts were adult males, adult females, juveniles, and pups. Error bars indicate standard deviations.

Table 2

Split-sample frequency of occurrence (SSFO) and estimated metric tons (t) of prey consumed by major prey group (family, order, or class) and by the lowest identifiable taxonomic group (indented) for prey consumed by Steller sea lions (*Eumetopias jubatus*), based on examination of scat samples collected from 2010 through 2013 in northwest Washington. Numbers of different types of scat samples by season are also provided. The SSFO calculations for major prey groups and for the lowest identifiable taxonomic groups were performed separately and, as a result, produced slightly different values.

	Total		Spring		Summer		Fall		Winter	
Sample type	No. of samples									
Scat samples	776		197		247		196		136	
Samples containing identifiable prey	730		185		230		183		132	
Samples containing no identifiable prey	41		11		15		12		3	
Empty samples	5		1		2		1		1	
Prey consumption	11,327 t		2998 t		2039 t		3821 t		2469 t	
Prey group	SSFO	t	SSFO	t	SSFO	t	SSFO	t	SSFO	t
Herrings, shads, sardines: family Clupeidae	22.7%	2573.8	13.8%	413.8	36.7%	747.6	21.0%	802.2	13.3%	329.0
Clupeids, unidentified	11.3%	1278.3	9.3%	278.2	15.2%	309.4	10.7%	409.0	8.1%	200.6
Pacific sardine (*Sardinops sagax*)	6.6%	748.5	0.0%	0.0	18.5%	378.1	3.0%	113.2	0.1%	3.1
Pacific herring (*Clupea pallasii*)	3.9%	440.5	2.6%	79.4	3.0%	60.9	6.2%	236.0	4.0%	99.5
American shad (*Alosa sapidissima*)	1.3%	144.6	1.9%	57.0	0.1%	2.2	1.9%	73.8	1.5%	37.7
Rockfishes: family Sebastidae	13.9%	1579.6	17.9%	537.4	8.3%	168.3	8.5%	325.8	25.8%	637.0
Rockfishes (*Sebastes* spp.)	13.8%	1567.0	17.7%	531.7	8.2%	168.0	8.4%	319.6	25.7%	634.6
Skates: family Rajidae	13.1%	1480.8	15.8%	473.0	9.2%	186.6	10.7%	407.2	19.5%	480.6
Skates, unidentified	12.7%	1442.6	15.5%	463.2	8.8%	179.4	10.2%	388.8	19.3%	477.6
Salmon: family Salmonidae	11.7%	1329.5	12.6%	377.1	5.8%	117.9	15.4%	588.9	15.8%	391.1
Salmon or trout, unidentified	11.6%	1315.4	12.6%	377.1	5.7%	116.1	15.1%	577.6	15.7%	388.0
Flatfishes: order Pleuronectiformes	9.7%	1100.5	8.8%	264.0	15.0%	305.9	10.1%	385.3	1.3%	31.4
Starry flounder (*Platichthys stellatus*)	4.4%	492.9	4.1%	123.4	6.9%	140.7	4.4%	167.7	0.2%	4.7
Righteye flounders, family Pleuronectidae	2.0%	225.4	1.8%	55.1	2.3%	46.0	3.0%	113.7	0.4%	9.4
Arrowtooth flounder (*Atheresthes stomias*)	1.3%	152.6	1.0%	29.4	3.2%	64.9	0.4%	14.6	0.0%	0.0
Flatfishes, unidentified	0.9%	97.1	0.7%	19.9	1.2%	25.1	0.9%	33.8	0.4%	10.9
Butter sole (*Isopsetta isolepis*)	0.6%	70.0	0.5%	14.0	1.1%	23.0	0.6%	21.8	0.0%	0.0
Rex sole (*Glyptocephalus zachirus*)	0.3%	38.9	0.0%	0.0	0.6%	11.5	0.6%	23.1	0.1%	1.9
Sanddabs (*Citharichthys* spp.)	0.3%	30.0	0.2%	7.3	0.2%	4.4	0.5%	20.6	0.0%	0.0
English sole (*Parophrys vetulus*)	0.2%	27.4	0.6%	18.9	0.0%	0.0	0.3%	10.4	0.1%	1.9
Dover sole (*Microstomus pacificus*)	0.2%	26.1	0.4%	13.2	0.2%	3.5	0.1%	3.5	0.2%	5.6
Sand sole (*Psettichthys melanostictus*)	0.1%	8.3	0.3%	8.6	0.0%	0.0	0.0%	0.0	0.0%	0.0
Slender sole (*Lyopsetta exilis*)	0.1%	6.5	0.0%	0.0	0.2%	3.7	0.0%	0.0	0.0%	0.0
Turbots (*Pleuronichthys* spp.)	<0.1%	3.9	0.0%	0.0	0.0%	0.0	0.1%	5.2	0.0%	0.0
Dogfish sharks: family Squalidae	8.3%	944.4	10.4%	311.3	5.6%	113.5	9.3%	355.5	9.0%	221.2
Pacific spiny dogfish (*Squalus suckleyi*)	8.2%	933.4	10.4%	310.5	5.5%	112.3	9.1%	347.0	8.9%	219.0
Hakes: family Merlucciidae	5.9%	663.7	0.9%	26.2	10.9%	222.2	8.6%	329.0	0.3%	6.2
Pacific hake (*Merluccius productus*)	5.8%	655.0	0.9%	26.2	10.8%	219.9	8.5%	322.9	0.3%	6.2
Cods: family Gadidae	4.8%	540.0	9.0%	270.4	1.7%	35.3	3.6%	138.6	5.7%	140.2
Cods, unidentified	2.1%	234.0	3.5%	105.1	0.6%	12.4	1.7%	65.8	3.1%	75.6
Walleye pollock (*Gadus chalcogrammus*)	1.4%	154.4	5.1%	152.6	0.0%	0.0	0.3%	11.1	0.0%	0.0
Pacific cod (*Gadus macrocephalus*)	1.2%	141.2	0.4%	10.5	1.0%	20.2	1.6%	60.0	2.5%	61.6
Pacific tomcod (*Microgadus proximus*)	<0.1%	3.9	0.0%	0.0	0.1%	2.2	0.0%	0.0	0.0%	0.0
Anchovies: family Engraulidae	2.1%	234.6	2.1%	62.0	1.9%	39.2	2.8%	107.9	1.3%	32.0
Northern anchovy (*Engraulis mordax*)	2.0%	230.5	2.1%	62.0	1.8%	37.7	2.8%	105.8	1.3%	32.0
Greenlings: family Hexagrammidae	1.7%	191.7	2.2%	64.6	0.6%	12.9	2.6%	99.6	1.6%	40.2
Lingcod (*Ophiodon elongatus*)	1.1%	124.7	2.1%	63.7	0.6%	11.4	1.3%	49.5	0.3%	8.4
Hexagrammids, unidentified	0.4%	48.9	0.0%	0.0	0.0%	0.0	0.8%	30.3	1.3%	31.8
Atka mackerel (*Pleurogrammus monopterygius*)	0.1%	14.7	0.0%	0.0	0.0%	0.0	0.5%	19.8	0.0%	0.0
Squids and octopuses: class Cephalopoda	1.1%	129.5	0.8%	23.9	0.4%	8.1	2.2%	82.9	1.5%	37.1
Squids and octopuses, unidentified	0.8%	89.6	0.5%	14.5	0.2%	3.7	1.5%	58.3	1.3%	31.3

(*Continued on next page*)

Table 2 (*continued*)

	Total		Spring		Summer		Fall		Winter	
Prey group	SSFO	t	SSFO	t	SSFO	t	SSFO	t	SSFO	t
Octopuses, unidentified	0.2%	24.7	0.1%	4.1	0.2%	4.4	0.5%	17.6	0.0%	0.0
Squids, unidentified	0.1%	13.9	0.2%	5.4	0.0%	0.0	0.2%	6.5	0.2%	4.7
Sand lances: family Ammodytidae	1.0%	112.5	1.1%	33.5	0.9%	18.0	0.7%	28.0	1.4%	33.8
Pacific sand lance (*Ammodytes hexapterus*)	1.0%	111.8	1.1%	33.5	0.9%	17.6	0.7%	28.0	1.4%	33.8
Lampreys: family Petromyzontidae	0.8%	91.8	1.0%	29.3	0.4%	7.4	1.0%	40.0	1.0%	25.4
Lampreys, unidentified	0.5%	56.1	0.5%	16.2	0.4%	7.4	0.7%	26.1	0.4%	10.0
Pacific lamprey (*Entosphenus tridentatus*)	0.3%	35.2	0.4%	13.1	0.0%	0.0	0.4%	13.9	0.6%	14.8
Mackerels and tunas: family Scombidae	0.6%	68.5	0.0%	0.0	1.7%	34.7	0.3%	10.4	0.0%	0.0
Pacific chub mackerel (*Scomber japonicus*)	0.6%	65.2	0.0%	0.0	1.6%	32.8	0.3%	10.4	0.0%	0.0
Smelts: family Osmeridae	0.6%	65.0	0.5%	15.9	0.1%	2.2	1.0%	39.7	0.8%	19.8
Smelts, unidentified	0.6%	65.0	0.5%	15.9	0.1%	2.2	1.0%	39.7	0.8%	19.8
Eulachon (*Thaleichthys pacificus*)	<0.1%	1.9	0.0%	0.0	0.0%	0.0	0.0%	0.0	0.1%	2.3
Sticklebacks: family Gasterosteidae	0.4%	50.6	1.5%	46.5	0.0%	0.0	0.1%	5.2	0.1%	2.7
Threespine stickleback (*Gasterosteus aculeatus*)	0.4%	50.3	1.5%	46.5	0.0%	0.0	0.1%	5.2	0.1%	2.3
Poachers: family Agonidae	0.4%	45.8	0.5%	16.2	0.4%	8.9	0.3%	12.9	0.3%	6.2
Poachers, unidentified	0.3%	34.9	0.4%	12.2	0.4%	8.0	0.1%	5.6	0.3%	6.2
Sturgeon poacher (*Podothecus accipenserinus*)	<0.1%	3.1	0.0%	0.0	0.0%	0.0	0.1%	4.2	0.0%	0.0
Sculpins: family Cottidae	0.4%	42.6	0.4%	11.3	0.0%	0.0	0.7%	25.6	0.6%	15.3
Sculpins, unidentified	0.3%	36.2	0.4%	11.3	0.0%	0.0	0.5%	18.3	0.6%	14.2
Pacific staghorn sculpin (*Leptocottus armatus*)	<0.1%	5.2	0.0%	0.0	0.0%	0.0	0.2%	7.0	0.0%	0.0
Snailfishes: family Liparidae	0.3%	33.6	0.4%	10.8	0.4%	8.1	0.2%	7.0	0.2%	4.7
Snailfishes, unidentified	0.3%	29.5	0.2%	7.3	0.4%	7.7	0.2%	7.0	0.2%	4.7
Hagfishes: family Myxinidae	0.2%	17.9	0.4%	10.8	0.0%	0.0	0.2%	7.2	0.1%	2.7
Pacific hagfish (*Eptatretus stoutii*)	0.2%	17.1	0.4%	10.8	0.0%	0.0	0.2%	6.5	0.1%	2.3
Gunnels: family Pholidae	0.1%	10.3	0.0%	0.0	0.0%	0.0	0.0%	0.0	0.5%	12.5
Gunnels, unidentified	0.1%	10.3	0.0%	0.0	0.0%	0.0	0.0%	0.0	0.5%	12.5
Eelpouts: family Zoarcidae	0.1%	6.9	0.0%	0.0	0.0%	0.0	0.2%	9.3	0.0%	0.0
Eelpouts, unidentified	0.1%	6.9	0.0%	0.0	0.0%	0.0	0.2%	9.3	0.0%	0.0
Jacks: family Carangidae	<0.1%	5.2	0.0%	0.0	0.0%	0.0	0.2%	7.0	0.0%	0.0
Jack mackerel (*Trachurus symmetricus*)	<0.1%	5.2	0.0%	0.0	0.0%	0.0	0.2%	7.0	0.0%	0.0
Frogs and salamanders, class Amphibia	<0.1%	4.3	0.0%	0.0	0.0%	0.0	0.2%	5.8	0.0%	0.0
Frogs and salamanders, unidentified	<0.1%	4.3	0.0%	0.0	0.0%	0.0	0.2%	5.8	0.0%	0.0
Wolffishes: family Anarhichadidae	<0.1%	3.9	0.0%	0.0	0.1%	2.2	0.0%	0.0	0.0%	0.0
Wolf-eel (*Anarrhichthys ocellatus*)	<0.1%	3.9	0.0%	0.0	0.1%	2.2	0.0%	0.0	0.0%	0.0

Salmonidae (13.5%), Merlucciidae (11.3%), Sebastidae (9.3%), Squalidae (7.8%), and Engraulidae (5.0%) (Table 4).

For California sea lions, diet diversity was similar in spring and summer, but the diet was less diverse in fall (Table 3). There were large differences in the SSFO of some prey families between seasons. The 3 most dominant families of prey made up 58.6% of the diet of California sea lions in spring, 55.3% of the diet in summer, and 77.7% of the diet in fall. Consumption of Sebastidae dramatically declined in the fall to an SSFO of 2.0% from 20.5% and 22.8% in the spring and summer, respectively. Cephalopoda composed a primary prey group during spring (6.3%) and summer (8.4%) but were only 1.6% of the diet in fall. During the fall, 47.4% of the California sea lion diet was composed of Clupeidae, compared with 24.6% in spring and 20.5% in summer. Higher consumption of Clupeidae in the fall appears to be due to the consumption of Pacific sardine, which had an SSFO of 11.4% in the fall and was not present in the spring or summer.

For yearly comparisons of the diet of California sea lions, we used only data collected during the fall because samples were not collected in all seasons of each study year (Suppl. Table 6). Prey diversity was similar between years during the fall (Table 3). The SSFO of prey taxa varied between years. Consumption of Pacific hake declined from 23.4% and 18.0% of the diet in 2010 and 2011, respectively, to 4.6% in 2012, and consumption of northern anchovy declined from 10.7% and 7.1% of the diet in 2010 and 2011 to 2.2% in 2012. As the SSFO of Pacific hake and northern anchovy declined, California sea lions ate more Clupeidae (41.7% in 2010 versus 51.0% in 2012), such as Pacific sardine and American shad (*Alosa sapidissima*). Consumption by California sea lions of Salmonidae also increased

Table 3

Shannon–Wiener diversity index and Levin's niche breadth for prey of Steller sea lions (*Eumetopias jubatus*) (SSL) and California sea lions (*Zalophus californianus*) (CSL), within season and year, from examination of scat samples collected during 2010–2013 in northwest Washington. Corresponding 95% bias-corrected and accelerated bootstrap confidence intervals are provided in parentheses. Seasonal values are for samples collected during that season pooled across all years of study. Yearly values reflect all samples collected for all seasons pooled within that year.

Species	Period	Shannon–Wiener index	Levin's niche breadth
SSL	Spring	2.32 (2.27–2.40)	8.32 (7.87–8.96)
SSL	Summer	2.04 (1.97–2.13)	5.22 (4.68–5.87)
SSL	Fall	2.40 (2.34–2.49)	8.60 (8.00–9.44)
SSL	Winter	2.11 (2.03–2.24)	6.26 (5.69–7.01)
SSL	2011	2.23 (2.18–2.30)	7.00 (6.47–7.60)
SSL	2012	2.36 (2.32–2.44)	8.29 (7.90–8.83)
CSL	Spring	2.20 (2.10–2.34)	6.99 (6.01–8.40)
CSL	Summer	2.12 (2.04–2.25)	6.90 (6.09–8.21)
CSL	Fall	1.77 (1.67–1.90)	3.68 (3.17–4.24)
CSL	Fall 2010	1.66 (1.51–1.95)	3.88 (3.15–5.13)
CSL	Fall 2011	1.64 (1.48–1.83)	3.58 (2.84–4.49)
CSL	Fall 2012	1.76 (1.60–1.97)	3.34 (2.72–4.12)

each year during the fall from 11.6% of the diet in 2010 to 16.4% of the diet in 2012.

Dietary niche overlap

The Morisita–Horn index indicates significant dietary niche overlap between Steller and California sea lions. Using data from spring, summer, and fall pooled for all years of the study, we found significant dietary niche overlap between these species of sea lions (MH=0.88; 95% confidence interval [CI]: 0.85–0.91). Data pooled by season indicate significant overlap in spring (MH=0.82; 95% CI: 0.75–0.89), summer (MH=0.76; 95% CI: 0.66–0.86), and fall (MH=0.76; 95% CI: 0.69–0.83). There was also significant dietary niche overlap between the diets of California and Steller sea lions by year (pooling of all samples collected in spring, summer, and fall), with an MH of 0.77 in 2010 (95% CI: 0.65–0.91), an MH of 0.94 in 2011 (95% CI: 0.92–0.97), and an MH of 0.82 in 2012 (95% CI: 0.76–0.88).

Prey consumption

The average annual amount of prey consumed by Steller sea lions and California sea lions hauling out in northwest Washington from 2010 through 2013 was 11,327 t (SD 1600) and 9063 t (SD 4098), respectively. The amount of consumption was variable by season for both species; California sea lions had much higher consumption in fall than in other seasons (Fig. 4). In Tables 2 and 4, we report prey consumption by prey group and by lowest taxonomic group identified.

Discussion

Diet characterization

This study is the first one to describe the diets of California and Steller sea lions in northwest Washington. Like in past studies, we found that California and Steller sea lions eat diverse assemblages of prey that are seasonally and annually variable (Bailey and Ainley, 1981; Lowry et al., 1991; Merrick et al., 1997; Reimer and Brown[1]; Sinclair and Zeppelin, 2002; Weise and Harvey, 2008; Womble et al., 2009; Scordino[2]; Orr et al., 2011; Riemer et al., 2011; Waite et al., 2012; Sinclair et al., 2013; Wiles, 2015; Trites and Rosen[3]). Steller and California sea lions in northwest Washington have diets among the more diverse that have been reported for these species on the basis of diet diversity indices (Aurioles-Gamboa and Camacho-Ríos, 2007; Orr et al., 2011; Waite et al., 2012; Sinclair et al., 2013).

We expected seasonal fluctuations in the diets of Steller and California sea lions for migratory prey taxa, such as the Pacific hake, the Pacific sardine, and Pleuronectiformes (Eschmeyer et al., 1983; Demer et al., 2012; Malick et al., 2020), but other seasonal fluctuations in their diets were a surprise. Resident, nonmigratory prey taxa, such as Rajidae and Sebastidae, composed a larger portion of the sea lion diets in winter and spring than in summer and fall, likely a result of compensation for the reductions of seasonally available prey. We expected to see a marked increase in consumption of salmon during the summer and early fall when adult Salmonidae migrate through the project area to their natal rivers (Weitkamp and Neely, 2002; Weitkamp, 2010), as observed in other

Table 4

Split-sample frequency of occurrence (SSFO) and estimated metric tons (t) of prey consumed by major prey group (family, order, or class) and by the lowest identifiable taxonomic group (indented) for prey consumed by California sea lions (*Zalophus californianus*), based on examination of scat samples collected from 2010 through 2013 in northwest Washington. Numbers of different types of scat samples by season are also provided. The SSFO calculations for major prey groups and for the lowest identifiable taxonomic groups were performed separately and, as a result, produced slightly different values. The total annual prey consumption was calculated by multiplying the SSFO pooled across spring, summer, and fall by the total prey consumption estimate, including the winter estimate of 553 t.

	Total		Spring		Summer		Fall	
Sample type	No. of samples							
Scat samples	263		47		50		166	
Samples containing identifiable prey	251		46		47		158	
Samples containing no identifiable prey	9		1		3		5	
Empty samples	3		0		0		3	
Prey consumption	9063 t		1551 t		1267 t		5692 t	
Prey group	SSFO	t	SSFO	t	SSFO	t	SSFO	t
Herrings, shads, sardines: family Clupeidae	38.2%	3462.5	24.6%	382.2	20.5%	259.7	47.4%	2699.2
Pacific herring (*Clupea pallasii*)	13.5%	1219.4	12.0%	186.9	8.4%	107.0	15.4%	874.0
Clupeids, unidentified	13.0%	1181.4	10.0%	154.8	10.9%	138.6	14.5%	828.0
Pacific sardine (*Sardinops sagax*)	7.2%	652.1	0.0%	0.0	0.0%	0.0	11.4%	650.6
American shad (*Alosa sapidissima*)	6.1%	549.5	3.6%	55.4	1.4%	17.3	8.2%	466.0
Salmon: family Salmonidae	13.5%	1220.3	11.5%	178.7	13.9%	175.7	13.9%	791.7
Salmon or trout, unidentified	13.1%	1186.8	11.3%	175.3	13.8%	174.4	13.4%	763.8
Hakes: family Merlucciidae	11.3%	1026.7	9.1%	140.5	6.5%	82.9	13.4%	763.5
Pacific hake (*Merluccius productus*)	11.0%	996.7	8.9%	138.2	6.5%	82.9	12.9%	735.9
Rockfishes: family Sebastidae	9.3%	838.7	20.5%	317.5	22.8%	288.9	2.0%	111.4
Rockfishes (*Sebastes* spp.)	9.1%	829.1	20.0%	310.8	22.8%	288.3	1.9%	109.9
Skates: family Rajidae	1.9%	169.5	3.1%	48.4	3.1%	39.8	1.1%	64.2
Skates, unidentified	1.8%	162.2	2.8%	43.3	3.0%	38.4	1.1%	64.2
Dogfish sharks: family Squalidae	7.8%	702.6	9.4%	146.1	12.0%	151.6	6.0%	342.2
Pacific spiny dogfish (*Squalus suckleyi*)	7.6%	685.5	9.3%	143.9	12.0%	151.6	5.8%	327.6
Anchovies: family Engraulidae	5.0%	453.5	5.4%	84.3	1.9%	23.6	5.8%	330.8
Northern anchovy (*Engraulis mordax*)	4.8%	434.3	5.4%	84.3	1.8%	22.9	5.5%	312.6
Flatfishes: order Pleuronectiformes	4.0%	366.0	3.4%	53.4	5.7%	72.1	3.7%	211.7
Arrowtooth flounder (*Atheresthes stomias*)	1.5%	135.1	0.0%	0.0	3.1%	39.3	1.4%	82.3
Righteye flounders, family Pleuronectidae	0.9%	77.4	0.4%	5.6	0.3%	3.9	1.2%	66.0
Starry flounder (*Platichthys stellatus*)	0.7%	60.2	0.0%	0.0	2.1%	27.0	0.4%	24.0
Dover sole (*Microstomus pacificus*)	0.5%	49.3	1.2%	18.0	0.4%	5.4	0.4%	22.8
Sanddabs (*Citharichthys* spp.)	0.4%	34.3	1.0%	15.2	0.0%	0.0	0.3%	18.0
Flatfishes, unidentified	0.2%	21.7	1.1%	16.9	0.0%	0.0	0.1%	3.6
Rex sole (*Glyptocephalus zachirus*)	0.1%	7.2	0.4%	6.7	0.0%	0.0	0.0%	0.0
Squids and octopuses: class Cephalopoda	3.8%	341.9	6.3%	98.1	8.4%	107.0	1.6%	93.4
Squids and octopuses, unidentified	2.3%	210.1	4.1%	64.1	6.9%	87.4	0.4%	24.4
Octopuses, unidentified	1.1%	99.9	2.1%	32.3	1.5%	19.6	0.7%	39.0
Squids, unidentified	0.2%	15.6	0.0%	0.0	0.0%	0.0	0.3%	15.6
Cods: family Gadidae	1.9%	176.4	1.3%	19.7	3.6%	45.4	1.7%	94.3
Codfishes, unidentified	1.1%	102.3	1.2%	18.0	1.6%	20.7	1.0%	55.2
Pacific cod (*Gadus macrocephalus*)	0.5%	41.3	0.0%	0.0	1.4%	17.3	0.3%	18.0
Pacific tomcod (*Microgadus proximus*)	0.2%	14.4	0.0%	0.0	0.4%	5.4	0.1%	7.2
Walleye pollock (*Gadus chalcogrammus*)	0.1%	12.0	0.0%	0.0	0.0%	0.0	0.2%	12.0
Smelts: family Osmeridae	1.5%	136.4	1.3%	20.3	0.0%	0.0	2.0%	114.4
Smelts, unidentified	1.4%	129.1	1.3%	19.7	0.0%	0.0	1.9%	107.8
Eulachon (*Thaleichthys pacificus*)	<0.1%	3.6	0.0%	0.0	0.0%	0.0	0.1%	3.6
Greenlings: family Hexagrammidae	0.5%	48.1	1.1%	16.9	0.0%	0.0	0.5%	30.0
Lingcod (*Ophiodon elongatus*)	0.3%	30.1	1.1%	16.9	0.0%	0.0	0.2%	12.0
Hexagrammids, unidentified	0.1%	12.0	0.0%	0.0	0.0%	0.0	0.2%	12.0

(*Continued on next page*)

Table 4 (*continued*)

Prey group	Total		Spring		Summer		Fall	
	SSFO	t	SSFO	t	SSFO	t	SSFO	t
Eelpouts: family Zoarcidae	0.4%	36.1	2.2%	33.7	0.0%	0.0	0.0%	0.0
Eelpouts, unidentified	0.4%	36.1	2.2%	33.7	0.0%	0.0	0.0%	0.0
Sand lances: family Ammodytidae	0.2%	21.1	0.0%	0.0	1.2%	15.7	0.0%	0.0
Pacific sand lance (*Ammodytes hexapterus*)	0.2%	21.1	0.0%	0.0	1.2%	15.7	0.0%	0.0
Lampreys: family Petromyzontidae	0.2%	21.1	0.7%	11.2	0.0%	0.0	0.2%	9.0
Pacific lamprey (*Entosphenus tridentatus*)	0.2%	18.1	0.7%	11.2	0.0%	0.0	0.1%	6.0
Jacks: family Carangidae	0.2%	18.1	0.0%	0.0	0.0%	0.0	0.3%	18.0
Jack mackerel (*Trachurus symmetricus*)	0.1%	13.5	0.0%	0.0	0.0%	0.0	0.2%	13.5
Sculpins: family Cottidae	0.1%	9.0	0.0%	0.0	0.0%	0.0	0.2%	9.0
Sculpins, unidentified	0.1%	7.2	0.0%	0.0	0.0%	0.0	0.1%	7.2
Snailfishes: family Liparidae	0.1%	9.0	0.0%	0.0	0.0%	0.0	0.2%	9.0
Snailfishes, unidentified	0.1%	9.0	0.0%	0.0	0.0%	0.0	0.2%	9.0
Hagfishes: family Myxinidae	0.1%	6.0	0.0%	0.0	0.4%	4.5	0.0%	0.0
Pacific hagfish (*Eptatretus stoutii*)	0.1%	5.2	0.0%	0.0	0.3%	3.9	0.0%	0.0

pinniped studies (Womble et al., 2009; Walters et al., 2020). The diet of California sea lions generally met our expectation; whereas, the portion of Salmonidae in the diet of Steller sea lions was smaller in summer than in winter by a factor of 3.

Annual variability in the diets of both sea lion species were also observed. Large annual differences in the portion of the diet composed of Pacific sardine and Pacific hake were likely driven by environmental factors that affect their distribution (Demer et al., 2012; Malick et al., 2020). We had expected to see a large increase of Salmonidae in the diet of both sea lion species during 2011 because of the presence of odd-year pink salmon (*Oncorhynchus gorbuscha*), which contributed to the roughly 6 times more Salmonidae fish entering Puget Sound in 2011 than in 2012 (Losee et al., 2019). Despite higher availability of Salmonidae in 2011, the portion of diet composed of Salmonidae was slightly higher in 2012 than in 2011 for both sea lion species.

Pacific hake composed a smaller portion of the sea lion diets than expected. From their studies of California and Steller sea lion diets in Washington in the 1990s, Scordino[2] and Wiles (2015) reported that bones of Pacific hake had an FO of 89.0–98.0%, compared with an FO of 15.0% for Steller sea lions and an FO of 30.6% for California sea lion in our study (Suppl. Table 1). The large decrease over time in importance of Pacific hake in the diet of Steller sea lions was likely due to environmental factors that resulted in a smaller portion of the population of Pacific hake utilizing northwest Washington during our study (Malick et al., 2020). During 2010–2013, the period of our study, the Makah Tribe's commercial Pacific hake fishery, which is spatially restricted to northwest Washington within 40 nmi (74 km) of shore, also had lower than normal landings (Svec[7]). Low availability of Pacific hake likely resulted in greater consumption by both Steller and California sea lions of prey that are species of conservation concern, such as rockfish and salmon species.

Biases in our study method may have resulted in inaccuracies in our diet estimations. The annual and seasonal variability in diet may be an artifact of our sampling effort (Trites and Joy, 2005). We often had only 1 or 2 sampling occasions per season for California sea lions and between 1 and 6 sampling occasions per season for Steller sea lions, and this effort may have resulted in detecting short-term shifts in fish distributions and

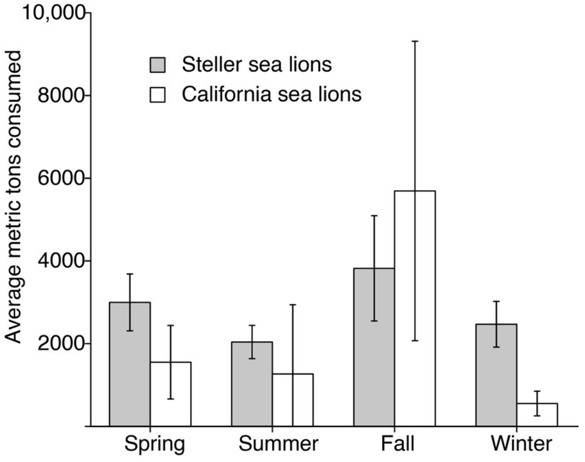

Figure 4

Estimated metric tons of prey consumed by Steller (*Eumetopias jubatus*) and California (*Zalophus californianus*) sea lions per season during 2010–2013 in northwest Washington. Error bars indicate standard deviations.

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[7] Svec, R. 2021. Personal commun. Makah Fish. Manage., Makah Tribe, 150 Resort Dr., Neah Bay, WA 98357.

availability that were not representative of seasonal or annual trends. However, in a study of penguin diet, frequent samplings with small collections were compared to infrequent samplings with large collections, and no significant differences in diet estimates were found (Berrow et al., 1999). Additionally, we chose to use SSFO to document diet; however, other approaches, such as biomass reconstruction, have been proven to have more accurately reconstructed the diet of sea lions (Tollit et al., 2007). The use of SSFO in our study may have resulted in overreporting the importance of small-bodied prey and underreporting the importance of large-bodied prey (Laake et al., 2002; Tollit et al., 2007).

Prey consumption

We estimated that Steller sea lions ate an average of 11,327 t (SD 1600) of prey per year and that California sea lions ate an average of 9063 t (SD 4098) of prey per year from 2010 through 2013 in northwest Washington. It is important when considering this result to remember that the scope of inference of this study was limited to sea lions hauled out in northwest Washington in 2010–2013. From 2010 through 2018, the average count of California and Steller sea lions hauled out in northwest Washington increased at a rate of 7.8% and 7.9%, respectively (Allyn and Scordino, 2020). At these observed rates of increase, our estimate of prey biomass consumed is likely less than half of what the 2 sea lion species are eating per year at the time of this publication.

Results from our model of consumption of prey by sea lions are best characterized as estimates rather than as definitive values for a number of reasons. First, we used published estimates for many parameters of the model. The proportion of body weight eaten per day published by Winship et al. (2006) is based on an energetic model with fixed caloric density of prey, although caloric densities are known to vary between species (Logerwell and Schaufler, 2005) and within species because of reproductive state and environmental factors (von Biela et al., 2019). Winship et al. (2006) did not account for fluctuations in caloric demands, but results from captive studies indicate that caloric demands of both Steller and California sea lions change seasonally (Kastelein et al., 1990, 2000).

We used haul-out count correction factors in our model that were developed for aerial surveys of sea lions (Lowry and Forney, 2005; Olesiuk[4]), although in our study, counts were conducted by vessel or from land. Vessel- and land-based counts are known to be negatively biased, compared to counts from aerial surveys (Westlake et al., 1997); however, no correction factor was available to compare values produced with our count method to aerial counts. We also did not account for the possibility that sea lions hauled out at sites in Canada, such as Carmanah Point, could forage in the same area as the sea lions hauled out in northwest Washington. Together, not accounting for the negative bias of vessel-based and land-based counts and not accounting for sea lions from Canada likely negatively biased our estimates of prey consumption for both sea lion species in our study area by an unknown amount. Despite the limitations and assumptions needed for our model of consumption, we believe it provided important perspective for the role of Steller and California sea lions in the northern California Current Ecosystem.

Dietary niche overlap

We hypothesized that Steller and California sea lions would have dietary niche overlap because they are central place foragers (Womble et al., 2009) that utilize the same haul-out sites (Mate, 1975) and have similar physiological dive limits (Weise et al., 2010). Our findings indicate that the sympatric sea lion species use the same dietary niche and are therefore competing for prey resources, but there are a number of caveats to this conclusion. First, interpreting niche overlap analyses is difficult because both a finding of no dietary niche overlap and a finding of significant dietary niche overlap could be signs of competition (Litvaitis et al., 1996). Further, significant overlap can occur without competition if prey species are abundant (Szabó and Meszéna, 2006). The observed rapid increase in counts of sea lions at haul-out sites in northwest Washington (Allyn and Scordino, 2020) indicates that prey resources were not limiting during our study.

Another consideration is that we evaluated dietary niche overlap by using prey grouped to family or a higher taxonomic order, an approach that assumes that prey species within groupings by family or higher taxonomic order represented prey items that were identical (Greene and Jaksić, 1983; Krebs, 1999). Some families of fish have species with very different behaviors, distributions, and sizes that affect their vulnerability to predation by the 2 sea lion species. For instance, in Sebastidae, there are species that are pelagic and schooling, solitary and benthic, primarily distributed in nearshore waters, and primarily distributed in offshore slope habitat (Eschmeyer et al., 1983). Even when we documented that the sea lions were eating the same species of prey, they could have exploited different size classes of that species. In a study in the Barents Sea, ringed seals (*Pusa hispida*) and harp seals (*Pagophilus groenlandicus*) had almost complete niche overlap strictly on the basis of identification of prey species in scat samples (Wathne et al., 2000), yet a closer examination of prey remains revealed niche partitioning with harp seals diving deeper for larger fish of the same species. Although our results indicate significant dietary niche overlap, it is possible that the sea lions of the 2 species in this study were partitioning their dietary niches in a way that our study design could not detect.

Conclusions

We found that Steller and California sea lions in northwest Washington have similar diets with seasonal and annual variability, and we found significant dietary niche overlap between the 2 species. Currently, there is no evidence that the dietary niche overlap between Steller and California sea lions is affecting the population growth of either species, but it bears monitoring if prey resources become limiting. Many of the prey species consumed by California and Steller sea lions during this study are culturally, economically, and ecologically important species (Kaplan and Leonard, 2012; Surma et al., 2018; Atlas et al., 2021). The estimates of prey consumption by the 2 sea lion species highlight the potential for increasing abundances of Steller and California sea lions in northwest Washington to result in reductions in the number of fish available to future recreational, commercial, and subsistence fisheries (Weise and Harvey, 2005, 2008; Chasco et al., 2017; Walters et al., 2020). Future diet studies conducted at a decadal scale would be useful for evaluating the effects of changing pinniped populations and ocean conditions.

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